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RESEARCH NOTE

EXTERNAL MORPHOLOGY AND ULTRASTRUCTURE OF THE PREHENSILE REGION OF THE LEGS OF *LEIOBUNUM NIGRIPES* (ARACHNIDA, OPILIONES)

Keywords: Chemoreception, harvestmen, locomotion, setae

Species of harvestmen (Arachnida, Opiliones, Palpatores) in the family Sclerosomatidae frequently employ prehensile flexion of the telotarsus during locomotion. Kaestner (1968) described the ability of these arachnids to anchor themselves to objects such as blades of grass by wrapping their legs around these objects. We have observed both *Leiobunum nigripes* (Weed 1892) and *L. vittatum* (Say 1821) moving across surfaces by forming coils at the end of their legs, especially the second pair (Figs. 1–4). While moving across a smooth substrate, these harvestmen cast the coiled regions of their legs about until they catch on a structure. Similar strategies are also employed by harvestmen during climbing, with the exception being that once a purchase is obtained with a coil, the free legs often wrap around and climb up the anchored leg. In addition, we have also observed harvestmen in aggregations wrapping their legs around the legs of adjacent individuals (Fig. 2).

Movement of the legs in harvestmen has been hypothesized to occur through a combination of muscle action and a hydraulic pump mechanism (Shultz 1989; Foelix 1996). According to this hypothesis, hemolymph is pumped into the legs by contraction of either the musculi laterales or the endosternal muscles (the primitive condition: Shultz 1991) of the prosoma (Parry 1960), resulting in leg extension. For harvestmen, Shultz (1989) reported that the basitarsus and telotarsus of the leg are traversed by two tendons arising from muscles that are used to move the tarsal claw. The telotarsus is subdivided by numerous adesmatic joints (>50: Kaestner 1968) that impart a prehensile character to the tarsus when flexed (Figs. 5–7). Flexion at the adesmatic joints can occur only ventrally in *L. rotundum* (Latreille 1795) because the ventral joint membranes are shorter than the dorsal joint membranes (Kaestner 1968). In this paper we describe the external morphology and ultrastructure of the prehensile region of the legs of juveniles of *Leiobunum nigripes* (Sclerosomatidae).

We collected juvenile *Leiobunum nigripes* from Chicot State Park, Evangeline Parish, Louisiana on 8 March 1997 and housed them in screened aquaria for approximately one week prior to preservation. Within 48 h after molting, specimens were fixed in cold (4 °C) Trump's fixative (a mixture of sodium cacodylate buffer, formalin, and glutaraldehyde) overnight, rinsed in 0.2 M sodium cacodylate buffer (pH = 7.4) and postfixed in 2% OsO_4 for 90 min at room temperature. Specimens were then dehydrated in a graded ethanol series and chemically dried with hexamethyldisilazane (Nation 1983), mounted on aluminum stubs, and sputter-coated for 2 min with ~20 nm of gold. We examined and photographed these specimens with a JEOL 6300-F field emission scanning electron microscope at accelerating voltages of 15–20 kV.

Specimens examined with transmission electron microscopy (TEM) were fixed and dehydrated using the same protocol described above for scanning electron microscopy

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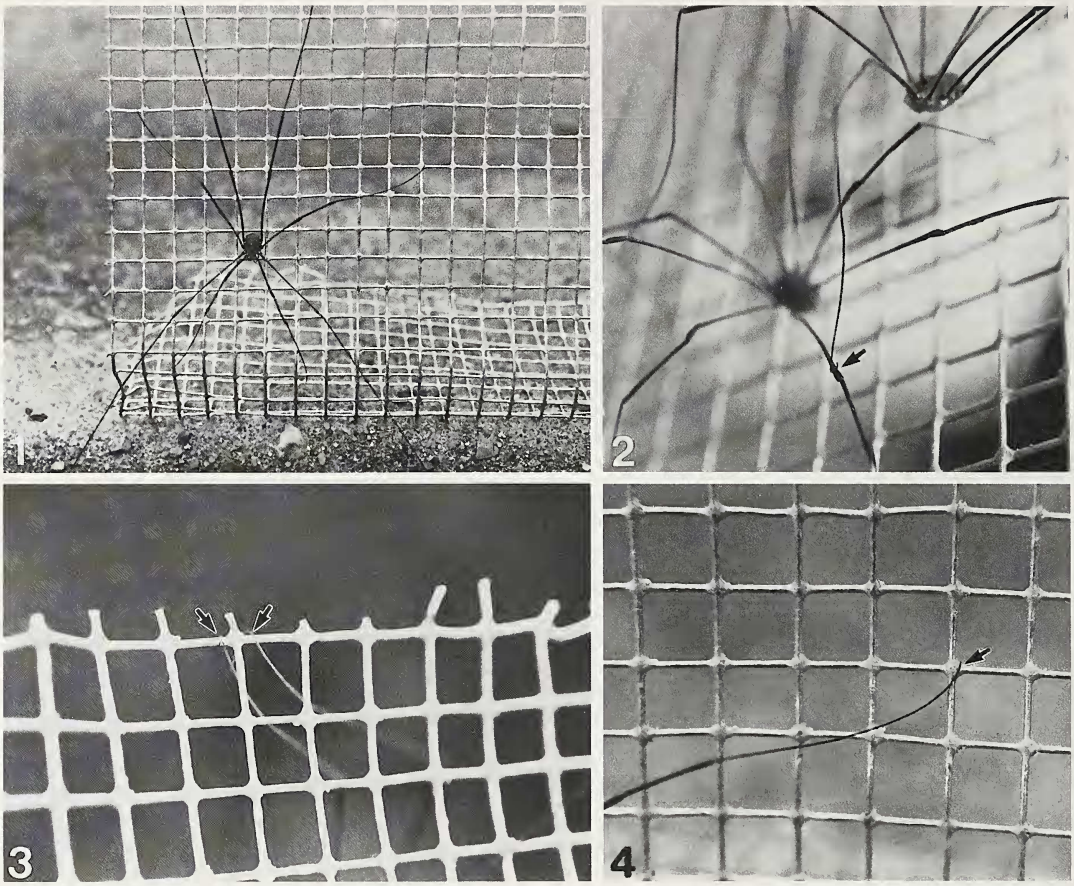
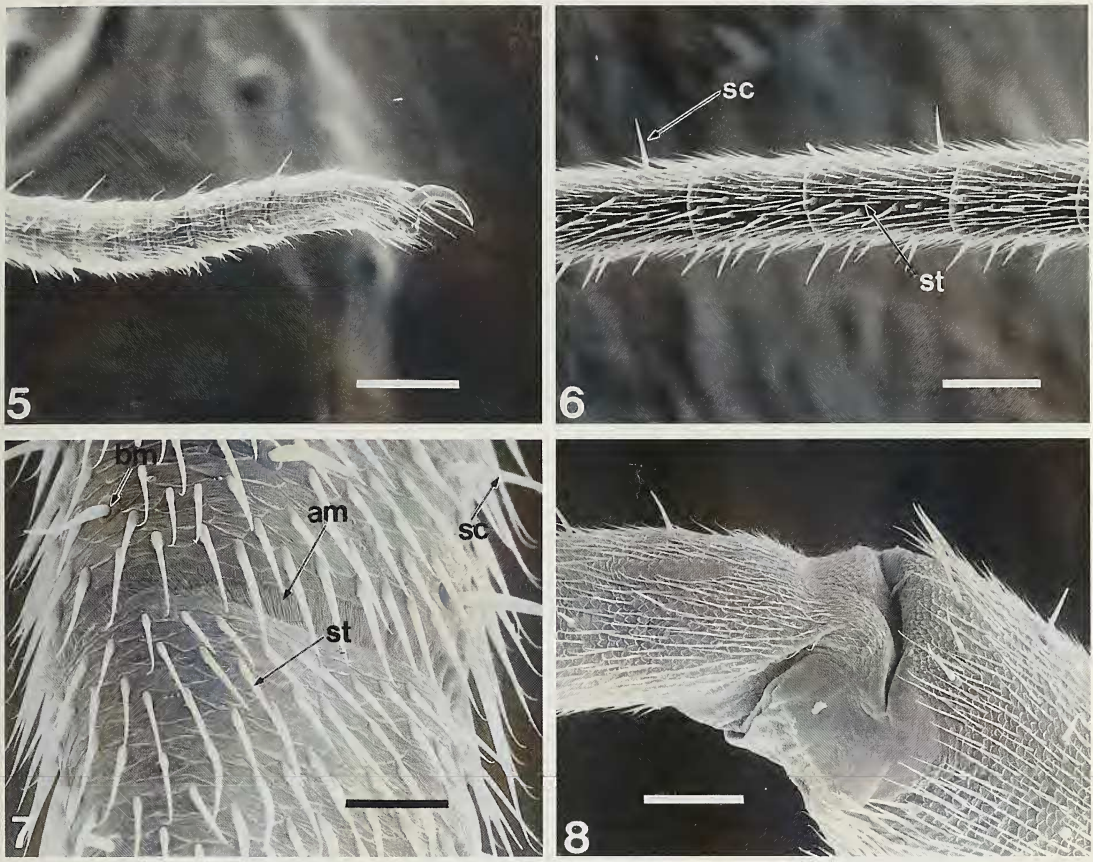


Figures 1–4.—Adults of the harvestman *Leiobunum nigripes* on hardware cloth (mesh size 6 mm × 6 mm) showing the prehensile ability of the tarsi. 1. An individual anchored to the substrate; 2. A small aggregation of harvestmen in which one individual has wrapped one of its leg around the leg of another; 3, 4. Dorsal views of the prehensile region of the tarsi, showing the wrapping of the legs around individual metal wires. Arrows in each figure indicate regions of flexion in the distal tips of the telotarsus.

(SEM). Following dehydration, specimens were slowly infiltrated in Spurr's low viscosity standard resin (Spurr 1969) over four days and sectioned with a diamond knife. Thin sections were collected on carbon-stabilized 200 μm thin bar grids, stained sequentially with methanolic uranyl acetate and aqueous lead citrate, and observed with a Hitachi H-7000 transmission electron microscope at 75 kV.

On each leg, *L. nigripes* has a single, smooth tarsal claw that is not toothed (Fig. 5). Smaller setae, or sensilla trichodea (Schneider 1964; Spicer 1987), and larger primary spines, or sensilla chaetica (Schneider 1964; Spicer 1987), are denser on the ventral surface of the telotarsus than on the dorsal surface (Fig. 6). The sensilla trichodea lie nearly parallel with the surface of the leg and have no specialized basal articulating membrane (Figs. 6, 7). The sensilla chaetica are nearly perpendicular to the leg surface and have a specialized basal articulating membrane (Figs. 11, 12), with blunt tips and whorled striae (Fig. 14), unlike those of sensilla trichodea (Figs. 6, 7). There is no evidence of trichobothria, mechanoreceptors that are common to most arachnids (Reissland & Görner 1986; Foelix 1996). The adesmatic joints are easily distinguished from true joints (Fig. 8) on the basis of their small size.

Cross sections examined with TEM confirmed the earlier anatomical observations of Kaestner (1968); i.e., no muscles were found between the segments of the telotarsus (Fig. 9). We observed only a single tendon (Fig. 9) connecting the tarsal claw to the claw-flexing

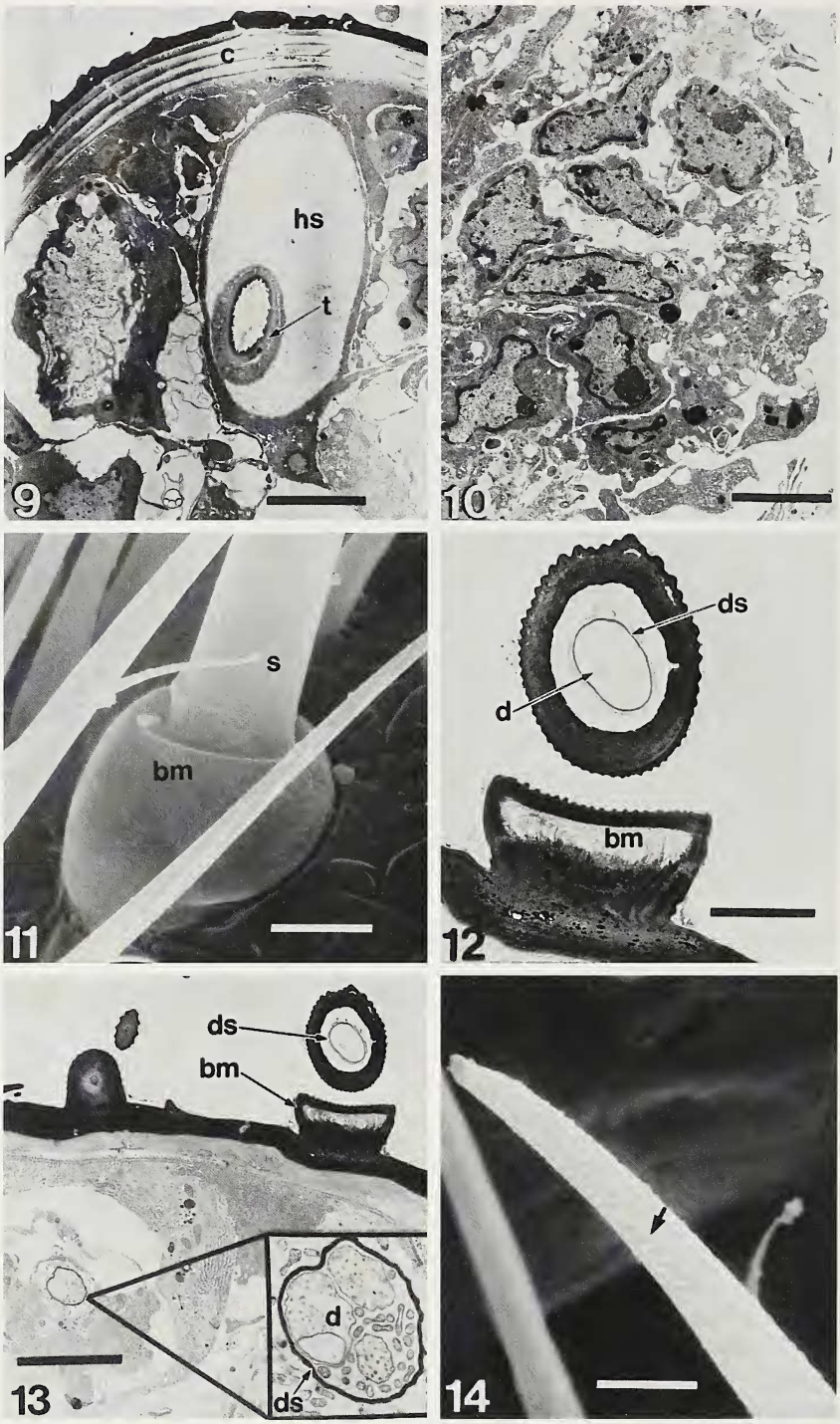


Figures 5–8.—External morphology of tarsus IV of *Leiobunum nigripes*. 5. Lateral view of the telotarsus and tarsal claw. Scale bar = 127 mm; 6. The adesmatic joints on the ventral surface of the telotarsus. Scale bar = 64 μm; 7. The sensilla trichodea (st) and sensilla chaetica (sc) on the ventral surface of the telotarsus near an adesmatic membrane (am) of an adesmatic joint. Scale bar = 23 μm; 8. A lateral view of a true joint between the two most distal segments of a leg, the basitarsus and the telotarsus. Scale bar = 73 μm.

musculature located in the tibia. In the telotarsus, we also observed epidermal cells lining the innermost portions of the cuticle (hypodermis) and occurring in clusters within the leg hemocoel (Fig. 10).

During the course of our TEM studies of the internal features of the leg, several sections provided information concerning the innervation of the sensilla chaetica (Figs. 6, 7, 11). Apical pores, a common feature of sensilla chaetica among arthropod chemoreceptors (reviewed in Zacharuk 1980), were not observed in our specimens. This sensillum is innervated by many presumably chemoreceptive dendrites (Figs. 12, 13). The dendrites originate from enveloping cells within the hypodermis (Fig. 13; inset) which do not attach to the cuticular wall of the basal articulating membrane. Instead, the sheath containing the dendrites passes directly through the center of the setal shaft (Fig. 12, 13), a common feature of arthropod chemoreceptors (Altner & Prillinger 1980; Zacharuk 1980).

The external morphology of the prehensile region of the legs of *Leiobunum nigripes* is similar to that reported by Kaestner (1968) for *L. rotundum* and by Holmberg & Cokendolpher (1997) for *Togwoteeus biceps* (Thorell 1877). Our observations of the sensilla on the tarsi of *L. nigripes* are also similar to those reported by Spicer (1987) for the palps of *L. townsendi*. The most numerous sensory organs on the legs of *L. nigripes* appear to be



Figures 9–14.—Ultrastructure of the telotarsus of leg IV of *Leiobunum nigripes*. 9. TEM micrograph of a cross section of the telotarsus revealing a single tendon (t) within a hemocoelic space (hs) and showing no muscle or tendon attachments with the inner surface of the cuticle (c). Scale bar = 6 μm; 10. TEM micrograph of the epidermal cells lining the innermost portion of the cuticle. Scale bar = 3 μm; 11. SEM micrograph of the specialized basal articulating membrane (bm) of a sensilla chaetica (s) from the ventral surface of the telotarsus. Scale bar = 3 μm; 12, TEM micrograph of a basal articulating membrane and shaft of a sensilla chaetica revealing the dendrites (d) and dendritic sheath (ds) within the shaft of the

sensilla chaetica (primary spines) and sensilla trichodea (setae). Unlike the palps of *L. townsendi*, however, these sensilla appear to be more numerous on the ventral surface of the telotarsus than the dorsal surface. Spicer (1987) also reported two types of sensilla chaetica (types I and II) based on the differing lengths of the sensilla. We observed only one type of sensilla chaetica in *L. nigripes*. We also did not observe any pores that are characteristic of chemoreceptors on the sensilla chaetica (Slifer 1970), but the structure of the dendrites innervating them (e.g., many dendrites and lack of attachment to the basal articulating membrane) indicates that they may function in chemoreception. Spicer (1987) inferred that the row of spines found on the ventral surface of the palps of *L. townsendi* were chemoreceptors and such receptors have been reported for other species of harvestmen (e.g., Foelix 1985).

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seta. Scale bar = 2 μm; 13. TEM micrograph of a sensilla chaetica, the cuticle and the underlying structure within the telotarsus. The inset is of a nerve from a chemoreceptive setae, revealing multiple dendrites within a single dendritic sheath. Scale bar = 5 μm; 14. SEM micrograph of the distal tip of a sensilla chaetica revealing the whorled striae on the external surface and the lack of a discernable pore at the tip. Scale bar = 3 μm.

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